Variation in reproductive success across captive populations: methodological differences, potential biases and opportunities

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Abstract

Our understanding of fundamental organismal biology has been disproportionately influenced by studies of a relatively small number of 'model' species that have been extensively studied in captivity. Laboratory populations of model species are commonly subject to a number of forms of past and current selection that may affect experimental outcomes. Here we examine these processes and their outcomes in one of the most widely used vertebrate species in the laboratory. The zebra finch (*Taeniopygia guttata*) is an important model species for research across a broad range of fields, partly due to the ease with which they can be bred in captivity. However, despite the amenability of zebra finches to captive conditions, we demonstrate extensive variation in the success with which different laboratories and studies bred their subjects, and only 64% of all females that are given the opportunity to breed, do so successfully. We identify and review several environmental, husbandry life-history and behavioural factors that are potentially contributing to this variation. The variation in reproductive success across individuals could lead to biases in experimental outcomes and drive some of the heterogeneity in outcomes across research groups. From this perspective, research on the captive zebra finch provides a useful case study of the wider problem caused by a failure to provide important contextual information supporting the empirical studies of animals. The zebra finch is an excellent system with which to conduct work in captivity and the aim of this review is to sharpen the insight that future studies of this species can provide, both to our understanding of this species and also with respect to the reproduction of captive animals more widely (important for conservation management). We hope to improve systematic reporting methods and further investigation of the issues we raise which will lead to advances in our fundamental understanding of avian reproduction as well as improving future welfare and experimental efficiency.

Introduction

There has been a recent call to improve on the reporting of information supporting empirical work conducted on animals to improve evaluation and interpretation, and facilitate the use of data in further work (Kilkenny, Browne, Cuthill, Emerson, & Altman, 2010). In their paper, Kilkenny et al., (2010) outlined the value of capturing contextual information (for example; animal backgrounds, housing and husbandry conditions, sample sizes and selection procedures) with a set of guidelines identifying 20 items that should be addressed in each publication. One of the main underlying drivers of this effort was to reduce the amount of clinical research using laboratory animals (through the UK based National Centre for the Replacement, Refinement and Reduction of Animals in Research). However, their paper Kilkenny et al., (2010) also highlighted the opportunities that are missed when the context of a particular study is not adequately communicated. Whilst their paper focused on all animal models, and particularly those used in biomedical research, there are also some clear messages for animal behaviour research. Furthermore, we believe that from the perspective of evolutionary biology, there are additional reasons for adhering to Kilkenny et al.'s (2010) recommendations as a result of biases in both experimental selection of subjects and evolutionary selection over both long and short time scales. Here we outline these issues by focusing singularly on the zebra finch, but believe that our central message and recommendations are more broadly applicable to all species which have already been, or are to be taken from the wild into the laboratory as the focus of work over an extended period of time, including multiple generations. The issues that we are specifically focused on are those that arise from the challenge of breeding and maintaining animals in a way that captures the extent of natural variation as seen in wild populations, but in a controlled environment. Our findings

are therefore also relevant to those managing and designing captive breeding programs for the benefit of animal conservation.

In the wild, we do not expect all individuals in a population of birds to successfully reproduce in a given breeding season or even across a whole lifetime (Newton, 1998). In wild zebra finches the low level of reproductive synchrony across a population (Griffith, Pryke, & Mariette, 2009; Zann, Morton, Jones, & Burley, 1995) suggests that individuals are quite strategic about when they choose to breed. Still, in two well-monitored populations in the wild, reproductive attempts typically end in failure. For natural nests that are vulnerable to predation, only 11-35% of clutches resulted in fledged young (Griffith et al., 2009; Zann et al., 1995). Even when predation was reduced through the provision of nest boxes, only 53% of clutches resulted in fledged offspring (Griffith et al., 2009). The variation in reproductive success in the wild is an interesting question in evolutionary ecology that must ultimately reflect the individual optimisation of many naturally and sexually selected traits. Even in zebra finches that have been brought into captivity, protected from predators, living in comfortable environmental conditions, provided with an *ad libitum* supply of resources, many individuals fail to reproduce. Zebra finches are not the exception to the rule, most individuals brought into captive breeding programs from wild populations fail to reproduce to replacement (Lees & Wilcken 2009). This failure presumably reflects some of the same selective pressures to those in the wild as well as additional challenges of living in captivity. Wild animal populations continue to decline at alarming rates (Butchart et al 2010; Pereira et al. 2010), and conservation breeding is becoming an increasingly important tool to guard against extinction. Thus careful evaluation of reproductive failure seen in extensive, multi-institutional captive breeding programs, such as the zebra finch, and other model

systems, can provide valuable insight for the planning and design of conservation-focused captive breeding programs (e.g. Slade et al. 2014).

The variation in reproductive success among captive birds is also interesting from an evolutionary ecology perspective, but is additionally worthy of attention due to the importance of the zebra finch as a model system for captive research. The zebra finch is a model species for research across a broad range of areas in evolutionary biology, physiology, animal behaviour, neurobiology and genetics (Griffith & Buchanan, 2010; Zann, 1996). One of the reasons it has been so widely adopted as a model species is the relative ease with which it breeds in the laboratory. Zebra finches reach sexual maturity within three months of hatching and adults are capable of reproducing repeatedly, and throughout the entire year under the right conditions of housing and food (Zann 1996). Research scientists and aviculturists recognized it as the easiest songbird to maintain and breed in captivity; often breeding is so robust that it can only be stopped by separating the sexes or removing all nesting sites. Nevertheless, there is considerable anecdotal evidence that large variation in reproductive success exists among individuals and populations of captive zebra finches. Not all respond similarly when given the opportunity and resources to reproduce. While some individuals quickly and repeatedly reproduce regardless of the circumstances, others fail to reproduce at all over a lifetime in captivity. The variance in reproductive success among individuals within a single population has been the explicit target of a small number of studies (e.g. Alonso-Alvarez et al., 2006; Bolund et al., 2009; McCowan et al., 2014). However, this variation is largely ignored and individuals that do not reproduce well are either deliberately or inadvertently selected out of populations and experiments alike. Typically studies focused around reproduction will report the sample size of pairs that bred and are included in specific

analyses. Sometimes a reference is made to additional birds that were given the opportunity but did not lay eggs (e.g. in Gorman et al. 2005, 77% of females produced a clutch), but more often studies report on the pairs that bred but make no mention of any additional birds. Even among those individuals that initiate a reproductive attempt there is variation in their ability to hatch eggs and rear offspring through to independence. Only rarely is this variation specifically the focus of analysis or comment, even in papers that are focused on aspects of reproductive behaviour or physiology. The variation in these aspects of individual reproductive success in domesticated populations will affect the number of offspring that an individual leaves in subsequent generations. As a result, the underlying determinants of this variation are subject to sexual, natural, and artificial selection. Some of these variables may have been maintained in a fairly constant state for over a hundred generations in captivity and have the potential to cause evolutionary change.

Our aim is firstly to summarize the extent of variation in the level of reproductive success in domesticated zebra finches across multiple research populations. While these estimates are unsuitable for directly measuring the extent of selection (because they will not represent lifetime reproductive success), they will provide a first indication of the extent to which selection might be acting in such populations and the extent to which it will vary between them. The level of contemporary selection is not only important in how it may affect change across generations in various traits, but also through the extent to which it will affect the composition of experimental datasets. For example, if there is consistent individual variation in an individual's likelihood of laying eggs after a given number of days (when presented with an opportunity to breed) then the selective pressure will be determined by the amount of time that investigators give birds in which to breed. For

example as illustrated by a hypothetical situation in Figure 1, an experimental cut-off 15 days after individuals are given the opportunity to breed will create a systematic bias with respect to a trait that is significantly related to the latency to lay. In this case, individuals in category 1 will have mostly laid by this time and will be well sampled, while individuals in category 2 will on average start laying later and only half of these birds will have laid by the time of the experimental cut-off. Here the categories might be an ordinal trait such as experience, or a continuous trait such as bill colour divided into two classes. The timescale and the trait itself are just illustrative of any situation in which an experimental time point is applied, so that individuals end up separated according to their breeding latency. The bias here will determine the composition of the sample for work focusing on aspects of biology after the cut-off. For example, if the research focuses on parental care, then the data will only be gathered on the subset of birds that have bred before the experimental cut-off is reached. It will also affect the composition of subsequent generations if the cut-off determines which individuals produce offspring and which do not. There are anecdotal reports that finch breeders only breed females that quickly lay eggs when given a male to breed with, and in the same way this may have affected selection over many generations of domestication. There are many logistical reasons why experimental cut-offs are used and they are probably reasonably widespread. We are not criticising the use of such cut-offs, but raising an awareness of the biases that they may introduce.

The other obvious source of experimental and population bias is where variation in reproductive success is significantly related to variation in traits such as behaviour or morphology (i.e. natural or sexual selection). Such a relationship will result in larger numbers of offspring being produced by a subset of the adult population, affecting the composition of the population over time. It may also result in biases in

experimental samples if an outcome requires the production of a certain number of surviving offspring. For example, if the end point of research is to compare either sons and daughters, or extrapair and within-pair offspring that survive to a certain age then we would be more likely to get data from pairs that produce larger broods. If we can start to develop an awareness of such biases it will help us in the interpretation of results (and variation across studies) and also enable us to control and reduce such bias in future studies.

Our second aim is to review areas of zebra finch biology that might help to explain variation in the extent to which individuals breed and produce recruits in laboratory populations. We believe that these areas offer good opportunities for further exploration and suggest that this might be best done by taking advantage of the many laboratories currently working with this species, through collaborative efforts that provide both variation and the replication of key variables. Future work could examine sources of variation in reproductive success by controlling for variation across populations while attempting to systematically alter just one or two variables at a time. Given the extensive molecular resources becoming available for this species (Warren et al. 2010), we also have the opportunity to test predictions concerning differences between domesticated and wild populations across a variety of traits that have been subject to directional selection in captivity.

The zebra finch remains an excellent model system with which to conduct work both in the wild and in captivity and the aim of this review is to sharpen the insight that future studies of this species can provide. To this end, our review highlights the variation that exists across study populations and indicates the potential biases that may occur as a result of biased sampling and breeding. Ultimately, consideration of this variation may provide insight into key traits that have been altered through the

process of domestication over the past hundred years. We believe it is important to draw attention to the fact that experimental outcomes in this species may arise from the different environments in which they are conducted (e.g. Rojas Mora & Forstmeier 2014).

PART I - The reproductive success of zebra finches in laboratories

Methods – We contacted laboratories in North America, Europe and Australia that have published research focused on zebra finches in the past ten years to request their involvement in this study. From those laboratories that responded positively, data were compiled in an effort to address the following: what proportion of females produce a) eggs and b) fledglings, when given the opportunity to breed? For these same pairs we also report whether they were in a cage or aviary, whether they were force paired or free to choose partners, as well as whether they originated from wild stock or domestic stock. Contributors provided data from their records, and none of this data was the result of work targeted just to assess proportional reproductive success. This breeding data was collected as part of researchers' independent on-going research with this species and was conducted in line with their own animal ethics approvals and the legal requirements of their respective countries. We collated data from situations in which birds were not subject to experimental manipulations that would have significantly affected reproduction. In some cases, broods were switched in cross-fostering experimental designs and we only used the data collected up to the point of the cross-fostering. A number of laboratories that have conducted work on zebra finches did not respond to our initial emailed communication and are therefore not represented, along with other laboratories that were unable to contribute data on these specific questions. Most of the data we have gathered and presented

focused on a set of individuals given a single opportunity to breed. However a couple of studies had allowed individuals to breed repeatedly over an extended period of time. The data provided by Varian-Ramos and Swaddle (from William & Mary College, US, and summarised in Table 2), provides us with an opportunity to assess the repeatability of reproductive success at an individual level. In their study Varian-Ramos et al. (2014) tracked a total of 33 individuals over a twelve month period in which they were allowed to breed ad libitum. The data used here is just from the control individuals in their study, that were not given the experimental treatment that is the focus of that work (Varian-Ramos et al 2014). In their study, clutches were removed 21 days after the last laid egg was laid if they failed to hatch, and offspring were removed from their parents when they reached independence. One clutch from each pair was removed as part of their study, but all other clutches were left for the parents to hatch and rear. This data provides important insight into the extent to which reproductive success and failure may be attributable to individual differences.

Statistical methods

Statistical analyses were focused on addressing individual repeatability of reproductive success, and characterising variation in reproductive success across and within populations, as well as investigating a couple of likely factors that might determine that variation. The percentage of females in each study that succeeded in clutch initiation and producing at least one fledgling in the across-study data set, and the percentage of breeding attempts per female that were successful in producing either fledglings or independent young in the data from William & Mary College, US; CW Varian-Ramos and JP Swaddle (Table 1) were transformed into binary data (i.e. 1: success, 0: failure) for all the analyses. Intra-class correlation (ICC) was calculated

for this success-failure outcome to examine the variability of reproductive success at the level of study and institution (across-study data), and individual (data from Varian-Ramos et al. 2014). The ICC in latent scale (link scale) was estimated based on generalized linear mixed models (GLMM) with a binomial distribution with logit link function. Models were fitted to the binary success-failure data. The latent scale ICC serves as a measure of variation in the response variable independent of its mean value, and is comparable across different sets of data (Nakagawa & Schielzeth 2010). The models included either identity of study, identity of institution, or identity of female as random effects. Effects of these three categorical variables were tested with generalized linear models (GLM). Differences between ICC estimates were examined based on posterior probability of difference (Bayesian P value). Models were fitted, and parameters were estimated with Markov chain Monte Carlo, using software Stan (http://mc-stan.org/) called from R package rstan (Stan Development Team. 2014).

Across experimental populations the method of assigning mating pairs differed between either force-paired or free choice pairs. The origin of experimental birds also varied between captive breed and wild derived. The effects of these two factors on clutch initiation and fledging success were investigated using GLMM with a binomial distribution and logit link function. In both cases, pairing type (forced vs. free choice) and origin of strain (domestic vs. wild) were included as fixed effects. Identity of study and identity of institution were included as random effects. Models were fitted using R package lme4 (Bates et al. 2015). Similarly, the effects of female age were examined using GLM with a binomial distribution and logit link function, and the difference between females (those who produced at least one fledgling) in the number of fledglings was examined with GLM with a Poisson distribution and log link function.

Results

Individual repeatability in reproductive success

Over a period of continual breeding (52 weeks) 33 females produced 316 clutches (mean = 9.58 ± 2.99 s.d.). In total 1670 eggs were laid (mean clutch size 5.32 ± 1.62 s.d.) and from these eggs 704 chicks hatched (mean per clutch 2.55 ± 1.66 s.d.). From these chicks 544 birds were fledged (mean per clutch 2.00 ± 1.52 s.d.; mean per female 16.48 ± 9.69 s.d.) and 461 independent were produced (mean per clutch 1.82 ± 1.51 s.d.). Overall just 42% of all eggs laid went on to hatch and just 28% of eggs produced an offspring that survived to independence. The correlation between the number of fledglings produced by each female and the number of independent offspring produced was strong ($r^2 = 0.87$, df = 138, t-value = 30.07, $P < 0.001$). However the correlation between the number of nestlings and fledglings produced was weaker ($r^2 = 0.55$, df = 177, t-value = 14.80, $P < 0.001$), and the correlation between the production of eggs and production of hatchlings was weaker still ($r^2 = 0.088$, df = 314, t-value = 5.51, $P < 0.001$).

Females differed in their likelihood of successfully producing fledglings (likelihood ratio test, $\chi^2 = 171.7$, df = 1, $P < 0.001$, n = 316); in the likelihood of producing independent offspring ($\chi^2 = 159.9$, df = 1, $P < 0.001$, n = 304); and also in the number of fledglings produced in successful broods (that produced at least one fledgling; $\chi^2 < 24.57$, df = 1, $P < 0.001$, n = 152, See Figure 2). The proportion of variation explained by inter-female differences was similar for the success in rearing young to fledging, and in rearing them to independence (for the production of fledglings, Intra-Class Correlation (ICC) = 0.56, s.e. = 0.095, n = 316 nests; and for

independent offspring, ICC = 0.53, s.e. = 0.094, n = 304; Bayesian P value, Pr (difference < 0) = 0.45).

Cross-study comparison of clutch and fledging success

From Table 1 we combined data from 23 institutions that provided data on egg hatching success per female and 21 institutions that provided fledgling rearing success per female. In total 2813 females out of 3213 successfully hatched chicks (proportion = 0.852, s.e. = 0.002), and 1889 females out of 2906 raised fledglings (proportion = 0.642, s.e. =0.003). The probability of females initiating at least one clutch varied across both studies ($\chi^2 = 5.12$, df = 1, P = 0.02, n = 3213) and institutions ($\chi^2 = 122.37$, df = 1, P < 0.01). Similarly, the probability of producing fledglings was different across studies ($\chi^2 = 13.36$, df = 1, P < 0.01, n = 2906) and across institutions ($\chi^2 = 325.9$, df = 1, P < 0.01, Figure 3). Inter-study variation for clutch initiation success (ICC = 0.28, s.e. = 0.055) was higher than inter-institution variation (ICC = 0.11, s.e. = 0.043; Pr (difference < 0) = 0.005, n = 3213 females), suggesting experimental conditions specific to individual studies explains more variation in egg laying than population level factors. The variability of fledging success was similar between the two levels of grouping (study: ICC = 0.27, s.e. = 0.04; institution: ICC = 0.19, s.e. = 0.06; Pr (difference < 0) = 0.14, n = 2906).

Reproduction and pair and female characteristics

Females were as likely to produce a clutch when force-paired or given free choice of partner (Wald test, z = 0.64, P = 0.52, n = 2885 females; Fig. 4a), and when from wild or domestic origin (z = -1.32, P = 0.19; Fig. 4b). In contrast, the proportion of females that produced fledglings was higher in domesticated strains than populations derived

from the wild more recently (z = 2.3, P = 0.021, n = 2578; Fig. 4c). Females that were force-paired by researchers had a lower fledging success than pairs formed through mate choice (z = -2.5, P = 0.011; Fig. 4d). For three institutions, females from two different age categories were bred and the classes could be compared (all else is presumed to be equal). In two of the three institutions young females had a greater reproductive success than older ones. In Lund (females of 9 versus 20 months) females were equally likely to produce a clutch (all females were successful, N = 56), and there was no difference in fledging success (z = 0.106, P = 0.92, N = 56). In Glasgow (females of 7 versus 43 months) younger females were more likely to produce a clutch (z = 3.57, P < 0.001, N = 1296), and produce fledglings (z = 5.62, P < 0.001, N = 1296). At the Max Planck (Seewiesen) there were comparative age classes across both domesticated and wild derived birds, allowing two separate comparisons. For domesticated birds (1.1 years versus 3.5 years) young birds had greater success at producing clutches (z = -4.214, P < 0.001, N = 328) and fledging offspring (z = -5.437, P < 0.001, N = 328). For wild derived birds, (10 versus 24 months) young females were also better at producing clutches (z = -1.028, P = 0.30, N = 114) and fledglings (z = -1.073, P = 0.28, N = 114).

Discussion

The data presented and the analysis conducted indicate that a significant percentage (around 35%) of females do not successfully produce offspring when given the opportunity to breed in these captive studies. This reproductive failure is partly due to the failure of abut half of these females to produce a clutch. For the remainder of females that produce a clutch, the primary determinant of reproductive failure is the ability to successfully hatch their eggs. However there is also failure to raise hatched

nestlings into fledglings and a much lower level of failure between fledging and the production of independent young. Some of the overall variation is determined by differences across institutions and also across separate studies within institutions. We also found strong evidence that the age of females is important in reproductive outcomes, with younger females being more successful than older ones. In addition, we found evidence that females that were free to choose their own partner were more successful than those to whom a partner had been assigned (force-paired), in line with a recent study that found free choosing females to have a 37% higher level of reproductive success (Ihle et al 2015).

Whilst the sample size was limited and there may be other confounding factors, we also detected some evidence for a higher level of reproductive success in domesticated birds than in laboratory populations that were from stock recently derived from wild-caught individuals. This result is consistent with the idea that selection has occurred, favouring traits that improve reproductive performance in captive conditions. We found strong evidence of intrinsic variation in individuals' ability to reproduce in the conditions they were provided, as would be required for selection to act. We found moderate intra-class correlation in reproductive success at the level of individual females, across all studies, and individual reproductive success was found to be repeatable in the longitudinal data from William and Mary College (Table 2, Figure 2). The latter data also illustrates how strong the selection is likely to be, with a large reproductive skew across the females monitored (although of course some of this may have been due to the male they were paired with).

It is important to be mindful that the data presented here were not collected systematically to address these issues. The heterogeneity in the data sets presented, and the context in which the captive populations were held sensibly precludes a

comprehensive investigation into the sources of variation in breeding success among these research laboratories. Nevertheless, we believe it is worthwhile to consider and highlight the potential sources of variation that might contribute, at least in part, to variation within and between populations in reproductive success of domesticated zebra finches. Specifically, we discuss: how differences in housing conditions and husbandry practices could contribute to differences in reproductive success between research laboratories; how individual responses to housing conditions can affect variation in reproductive success within laboratory populations; and the effects of variation in reproductive success on genetic diversity in populations of domesticated zebra finches.

PART II – Determinants of reproductive success in captive birds

1. Variation in housing conditions and aviculture practices

Many research laboratories keep birds in controlled rooms to remove the confounding effects of temperature, light and humidity variation on experimental work. Other sources of variation between research laboratories will also include differences in housing conditions and basic husbandry practices. All of these are likely to contribute to variation in reproductive success of domesticated zebra finches. In the wild, zebra finches are opportunistic breeders that use a range of environmental cues to optimize reproductive success. In contrast to the generally predictable and primarily photoperiod-dependent development of reproductive systems typical of seasonally breeding passerines (reviewed in Dawson et al. 2001; Sharp 2005), the reproductive axis of zebra finches is able to rapidly adapt to favourable breeding conditions – seemingly at any time of year – despite showing some seasonality to their reproduction (Perfito et al. 2006; Williamson et al. 2008; Zann 1996; reviewed in

Hahn et al. 2008). This breeding strategy has important bearing on domesticated zebra finches because slight variation in housing conditions (e.g. light regime, humidity, food quality, housing density) may have broad repercussions on breeding success. For example, photostimulation does affect testes size despite the opportunistic breeding pattern widely observed (Bentley, Spar, MacDougall-Shackleton, Hahn, & Ball, 2000). It is generally assumed that zebra finches (as opportunistic breeders) remain at a constant state of breeding readiness given "good" environmental conditions, such as those provided in the laboratory studies, and breeding condition is rarely controlled for. However, field and laboratory studies indicate that individuals are not at a constant of breeding readiness, cycle through breeding and non-breeding periods, which correspond with distinct neuroendocrine states (Perfito, Zann, Bentley, & Hau, 2007; Prior, Heimovics, & Soma, 2013).

Indoor versus outdoor housing

Across studies, there is extensive variation in the basic housing conditions in which breeding birds are kept. For example, some populations of zebra finches are kept in partially outdoor aviaries (e.g.Burley 1986; Gilby et al. 2011; Ihle & Forstmeier 2013) while others experience only indoor conditions (e.g. Gorman & Nager 2003; Birkhead et al. 2006). Outdoor and indoor housing environments likely vary in temperature and humidity (see *Humidity and temperature),* light quality and quantity, as well as other factors that affect the health and well-being of captive breeding birds. For example, in poultry, individuals kept outdoors with direct access to sunlight are better able to synthesise vitamin D resulting in better growth and egg production (Lewis & Gous, 2009). The natural lighting of outdoor housing can also be less stressful for breeding birds compared to the artificial lighting of indoor housing that can cause an increase

in glucocorticoid stress hormones (see: *Stress Physiology*; Evans et al. 2012). Artificial lighting may also vary qualitatively across research laboratories depending on the total luminance and whether full daylight spectrum lights are used.

Housing in outdoor aviaries can also have negative effects on health and reproduction. For example, birds housed in outdoor aviaries may have greater exposure to inter-specific transmissions of pathogens resulting in higher levels of disease and morbidity (e.g. Brittingham et al. 1988). Natural weather conditions will be far more variable than indoor conditions, and also vary significantly with the local climate geographically. Extreme or unpredictable conditions (e.g. unexpected cold temperatures) could be stressful for breeding adults and nestlings, resulting in nest abandonment or nestling mortality (Lynn & Kern, 2014). However, natural weather conditions in the wild are also variable and may have important stimulatory effects.

Outdoor aviaries may also be subject to varying levels of environmental background noise depending on location, which might affect reproductive success (Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011). Finally, the type of housing tends to determine the number of birds that are held together (for example large groups in outdoor aviaries versus small groups in typically smaller indoor cages), which will also potentially confound attempts to understand the effects of indoor versus outdoor housing, for the reasons discussed below.

Housing and social effects

The composition and density of breeding groups of zebra finches might affect pair bonding and, in turn, reproductive success. Research in both domesticated (Adkins-Regan & Tomaszycki, 2007; Schweitzer, Schwabl, Baran, & Adkins-Regan, 2014), and wild zebra finches (Mariette & Griffith, 2012b) has focused on the importance of

the pair bond in this species for successful reproduction. These studies suggest that pairs that are well acquainted, phenotypically similar to one another, or with a high level of behavioural coordination differ from other pairs in a number of aspects of reproduction such as the time taken to initiate breeding or the number of offspring produced. However, there is variation across studies and in research populations in the way in which individuals can form and maintain pairs. Pairs are either allowed to form naturally in aviaries (free choice – but constrained as individuals become paired and are removed from the mating pool), or are determined by the experimenter as a male and female are placed in a cage together (force paired; Table 1 and references therein). In the zebra finch, females force-paired to preferred mates laid slightly more eggs or laid the first egg of their clutch sooner, compared to females paired with non-preferred mates (Balzer & Williams, 1998; Holveck & Riebel, 2010). In another estrildid species (the Gouldian finch *Erythrura gouldiae*) females forced paired with incompatible mates had long-term elevated levels of corticosterone (the dominant avian stress hormone; Griffith et al. 2011). Recently, Ihle et al. (2015) found in the zebra finch that freely chosen pairs achieved a 37% higher fitness than experimentally arranged pairs, a finding that is consistent with recent studies in captive bred zoo species that have shown that mating animals to their preferred partner, versus non-preferred or genetically assigned partners, dramatically increased reproductive success (Martin et al. 2012).

In addition to the potential stress caused by force pairing with a non-chosen partner, captive zebra finches also experience stress when separated from their partner during or at the end of experiments (Perez et al., 2012; Remage-Healey, Adkins-Regan, & Romero, 2003; Schweitzer et al., 2014), although some of this stress might have been due to the stress of social isolation itself. Breeding partners are often

separated at the end of experiments and birds are kept in single sex populations before pairing them at a later date with the same or a different partner for another experiment. In the wild, males and females form enduring partnerships and remain close to one another throughout the year (Mariette & Griffith, 2012b) with little evidence of infidelity (Griffith, Holleley, Mariette, Pryke, & Svedin, 2010) or divorce (Zann, 1996), although wild individuals will occasionally lose a partner to predation or natural mortality. Hence, elevated stress hormones caused by partner separation or forced pairing could contribute to reduced reproductive success in laboratories (see *Stress physiology*).

The wild zebra finch is a very social bird with groups of individuals often breeding closely together (Zann, 1996). It is likely that different housing conditions will affect the social conditions under which zebra finches breed in captivity. In aviaries, birds will be free to socially interact with many other individuals, whereas in cages, there is likely to be varying degrees of visual and acoustic communications between individuals in different pairs. There is some evidence from captive birds that reproductive investment is modified by acoustic signals from other members of a loose social group (Waas, Colgan, & Boag, 2005). This is consistent with the finding that in the wild, despite a low level of synchrony across a whole population, pairs nesting very closely to one another synchronise their reproductive activity (Mariette & Griffith, 2012a). However, whilst social contact can have stimulatory effects on some individuals, there may be inhibitory effects on others. In the wild, proximity to others shows great variation with many pairs actively choosing to breed away from colonies in solitary positions (Mariette & Griffith, 2012a). This may reflect an underlying behavioural polymorphism of social and asocial individuals, with the latter perhaps socially inhibited by the close proximity of others (Dall & Griffith, 2014).

Breeding in aviaries has the advantage of more closely resembling natural circumstances in which individuals and pairs can act as part of a social network and facilitate each other. However, the social situation in an aviary can create competition for nest sites, nesting material and food, which in turn might result in lower reproductive success for some parts of a population (McCowan et al., 2014).

Variation in the size and construct of social groups (through housing) will also have consequences for the development of social and sexual behaviour in offspring (Mariette, Cathaud, Chambon, & Vignal, 2013; Ruploh, Bischof, & Engelhardt, 2012). Reproductive success may be affected by the expression of song in adults, with key parameters of song structure (complexity, tempo, stereotypy) and output being affected by the environment (Brumm, Zollinger, & Slater, 2009; Holveck, Vieira de Castro, Lachlan, ten Cate, & Riebel, 2008) and by the availability of song tutors during early life (Derégnaucourt, 2011). The early environment also affects the development of song preference behaviour in females (Clayton, 1990b, 1990c; Riebel, Naguib, & Gil, 2009). There is some evidence of reduced variance in song structure between wild and domesticated populations (Slater & Clayton, 1991; Woodgate, Mariette, Bennett, Griffith, & Buchanan, 2012), and it is possible that there is variation in the quality or variance of song across captive populations. Variation in the expression of song across populations may contribute to heterogeneity in reproductive investment and behaviour given the importance of song in stimulating reproduction (Bolund, Schielzeth, & Forstmeier, 2012; Riebel, 2009; Woodgate et al., 2012).

Humidity and temperature

In wild zebra finches, the trigger of breeding activity has generally been related to rainfall (Zann et al., 1995). Other environmental cues such as humidity and temperature have been shown to both directly (Cynx, 2001; Vleck & Priedkalns, 1985), and indirectly (Williams, 1996a; Williamson et al., 2008) stimulate reproductive behaviour in zebra finches. Variation in humidity could be an informative cue for zebra finches as it is related to rainfall, and ground water conditions which influence both water and food availability. However, humidity is often not accounted for in captive studies and a relatively large range is often considered as constant (Table 1). For example, Williams (1996) considered humidity range of 35-55% as constant. Williamson et al. (2008) found seasonal patterns of maternal investment in birds breeding in 'constant temperature and humidity rooms' but suggest that the 40-60% variation in humidity in their study may have been the variable that could have influenced breeding if the birds are sensitive to such changes. Therefore, it appears important not to ignore even small changes in humidity, as there remains the possibility that variation in humidity in captive breeding environments can affect reproductive output. Unfortunately, it is very difficult to artificially control humidity to a high degree as air-heating systems typically deliver dry air, and typically humidity is not often controlled to a high level of precision independently of air temperature.

In addition to humidity, variation in temperature is likely to affect reproductive physiology and behaviour in ways that may contribute to variation in reproductive success. Although wild zebra finches have been recorded to breed throughout the winter in temperatures down to as low as 2.2°C (Zann et al., 1995), periods of low temperature are associated with a reduction or cessation of reproductive activity (Davies, 1977). Reproductive success in captive birds may be similarly affected by

variation in temperature, or across seasons. Captive birds kept at low temperature (7°C) increased food consumption and time to initiate egg laying and decreased the total number of eggs laid (Salvante, Walzem, & Williams, 2007). Furthermore, presumably due to the costs of thermoregulation, females reduce the amount of heat transferred to eggs during incubation in low temperature conditions (Nord, Sandell, & Nilsson, 2010).

Handling and disturbance

Laboratories may vary in a number of standard procedures relating to the provision of cover, the number of times birds are visited during the day, cleaning routines and the type of interaction that birds get, all of which may lead to different levels of disturbance and stress, which may ultimately result in inadvertent selection on stress-tolerant phenotypes. To date, there have been remarkably few studies investigating these issues in the zebra finch. In their paper, Collins et al. (2008) found that the provision of a food reward (fresh greens) directly after handling helped birds to settle more quickly. In the same study they also investigated the effect of providing cover (part of the cage was covered with an opaque cloth), but found that this actually increased the level of fearfulness over the timeframe of the experiment (Collins et al., 2008). Whilst Collins et al. (2008) did not look at reproductive performance in the context of these factors, they did find the handling regime (whether they were rewarded after capture) affected attractiveness in mate selection. The recent study by Sorge et al. (2014) demonstrates just how subtle the effects of handling or visiting stress can be on captive animals, with laboratory rodents of several species showing significantly different anxiety and pain responses in the presence of male versus female research technicians.

Diet and nutrition

The basic diet and nutritional supplements provided to breeding zebra finches vary across populations and also across studies within populations and are likely to influence variation in reproductive investment and success (Gorman & Nager, 2003; Patricia Monaghan, Metcalfe, & Houston, 1996; Williams, 1996b). In Table 1 we have summarised some examples of dietary variation across different studies and populations. It is standard practice to provide zebra finches with an *ad libitum* seed diet, but there can be substantial variation between the quality of seed with some diets fortified with vitamins and other supplements. In addition to seed, breeding zebra finches are often supplemented either daily or intermittently with more nutritious foods such as hard-boiled eggs and spinach (Table 1). The diet provided to zebra finches prior and during reproduction can have pervasive effects on reproductive success (and the variation is often intentionally experimental). Female zebra finches provided with a low quality diet produce smaller eggs, smaller clutches, have lower hatching success, fledge fewer young, and, overall, have lower lifetime reproductive success (Lemon & Barth, 1992; Rutkowska & Cichoń, 2002; Rutstein, Slater, & Graves, 2004; Rutstein, Gilbert, Slater, & Graves, 2004; Selman & Houston, 1996). In male zebra finches, diet quality can influence bill and plumage coloration, and courtship rate, all of which can affect female preference and reproductive investment (Atagan & Forst, 2012; Burley, Price, & Zann, 1992; McGraw, Gregory, Parker, & Adkins-Regan, 2003).

In addition to variation in diet quality, laboratories also vary in the manner in which food is provided to breeding zebra finches, which could influence reproductive success. For example, the number of outlets through which a given amount of food

can be accessed influences the acquisition of that food by individual birds (e.g. Broom & Ruxton 2003; Vahl & Kingma 2007) and large groups of birds in aviaries with a single food dispenser will have to compete much harder than pairs housed in small cages. As a result, in large aviaries, dominant individuals may have greater access to food. Access to food could affect reproductive success by influencing individual decisions about mass regulation (Cuthill, Hunt, Cleary, & Clark, 1997), the physiological ability of birds to breed (Rashotte, Sedunova, Johnson, & Pastukhov, 2001; Sandell, Adkins-Regan, & Ketterson, 2007),and the expression of condition-dependent sexually selected traits such as bill colour and song rate (Birkhead, Fletcher, & Pellatt, 1998; Pariser, Mariette, & Griffith, 2010).

Overall, we need to remain mindful that the zebra finch is highly opportunistic and is likely to adaptively respond to small variations in important environmental parameters such as housing conditions, temperature, humidity, nutrition, and social cues. As such, although many laboratories may attempt to maintain standard conditions of such parameters, variation between and within laboratories is likely to affect reproduction in ways that are currently not accounted for in most studies.

2. Individual responses

Variation in housing conditions and aviculture practices may explain differences in the degree of breeding success of populations of zebra finches *between* laboratories (Table 1). However, variation in breeding success *within* a population of interest is more likely driven by individual differences in behavioural and physiological responses to the particular housing, social, and dietary conditions and handling regimes of the population in question. In turn, intra-population variation in physiology and behaviour can be increased by housing practices or decreased due to inadvertent

artificial selection (see *Population genetics and artificial selection*). Overall, understanding how individual variation in physiology and behaviour affect reproductive success in captive populations of zebra finches is crucial to teasing apart mechanisms that explain large-scale differences in inter-population reproductive success.

Stress physiology

Individuals can vary substantially in their endocrine responses to environmental stimuli that can, in turn, cause dramatic variation in reproductive behaviours (e.g. Lendvai and Chastel, 2010). For example, in captive zebra finches, some individuals might be more susceptible to stressors associated with housing conditions such as cage conditions, population density, and exposure to caregivers. In birds, stressors activate the hypothalamic-pituitary-adrenal (HPA) axis and result in the release of the steroid hormone corticosterone (reviewed in Cockrem 2013). Corticosterone elicits physiological and behavioural responses that help birds prioritize self-maintenance and survival at the expense of reproduction (reviewed in Wingfield & Sapolsky 2003). Across bird species, corticosterone is associated with delayed clutch initiation (Griffith et al., 2011; Salvante & Williams, 2003), reduced incubation (Edwards, Chin, Burness, Gilchrist, & Schulte-Hostedde, 2013; Spencer, Heidinger, D'Alba, Evans, & Monaghan, 2010; Thierry, Massemin, Handrich, & Raclot, 2013), lower nestling provisioning (Almasi, Roulin, Jenni-Eiermann, & Jenni, 2008), greater nest abandonment (Spée et al., 2011; Strasser & Heath, 2013), and lower reproductive success (fewer offspring fledged; Schmid et al. 2013). In captive zebra finches, individual variation in stress responsiveness could be a mechanism that explains

variation in reproductive success within a population. In this scenario, birds that are least responsive to stressors will have the greatest reproductive success.

Stress responsiveness is both heritable and influenced by the early rearing environment (Adkins-Regan, Banerjee, Correa, & Schweitzer, 2013; Evans, Roberts, Buchanan, & Goldsmith, 2006; Spencer, Evans, & Monaghan, 2009), and perhaps most surprisingly even by the stress profile of their partners (Monaghan, Heidinger, D'Alba, Evans, & Spencer, 2012). If birds with low stress responses are more successful at breeding in captivity, this trait will be selected for over time, resulting in captive populations with dampened stress responses. Anecdotally, it is apparent that laboratory populations of birds that are very recently derived from wild birds are much more flighty than domesticated birds (Griffith, Buchanan and Forstmeier pers. obs.). Although not yet systematically explored in zebra finches, physiologically dampened stress responses have been documented in grey partridges (*Perdix perdix*) and white-backed munia (*Lonchura striata*) with wild-derived birds having higher stress responses compared to domesticated congeners (Homberger, Jenni-Eiermann, Roulin, & Jenni, 2013; Suzuki, Yamada, Kobayashi, & Okanoya, 2012). Corticosterone has broad pleiotropic effects on physiology and behaviour (Sapolsky, 2000). Inadvertent selection for individuals with low stress responses is likely to have organismal consequences beyond modifications in stress physiology.

Individual and population level HPA axis characteristics may provide a useful way of comparatively testing the deleterious physiological effects of potential sources of reproductive failure as reviewed herein. For example, studies using direct measures of corticosterone can evaluate the relative stress of widespread practices such as forced pairing (Griffith et al., 2011), mate separation (Perez et al., 2012; Remage-Healey et al., 2003), food restriction (Spencer et al., 2005), and housing conditions

such as artificial lighting (Evans et al., 2012; Maddocks, Goldsmith, & Cuthill, 2001). HPA axis characteristics have been used as a tool to diagnose the stressfulness of housing conditions and the efficacy of breeding programs in zoo animals (Scarlata et al., 2012; Shepherdson, Carlstead, & Wielebnowski, 2004), the effect of anthropogenic disturbance on reproductive success in free-living birds (Crino, Johnson, Blickley, Patricelli, & Breuner, 2013; Crino, Van Oorschot, Johnson, Malisch, & Breuner, 2011; Müllner, Eduard Linsenmair, & Wikelski, 2004; Walker, Boersma, & Wingfield, 2005), and the general welfare of captive animals (Fanson, Lynch, Vogelnest, Miller, & Keeley, 2013; Lane, 2006; Whitham & Wielebnowski, 2013). In summary, identifying the factors associated with housing and experimental procedures that cause stress (as indicated by elevated corticosterone) in breeding zebra finches will allow researchers to mitigate stressful practices and capture reproductive success across a wider range of phenotypes in captive populations, i.e. reducing the strength of selection for 'stressor-resistant" phenotypes.

Individual behavioural variation

A recent focus of work in behavioural ecology is the extent to which individuals differ consistently across time and/or context in behaviour – personality variation – and what selection pressures might maintain this variation (Wolf & Weissing, 2012). There is as yet little information on wild zebra finches, but domesticated zebra finches, like wild birds of other species, show variation across personality traits such as boldness, exploratory behaviour, activity, neophobia, and aggressiveness (Beauchamp, 2000; Brust, Wuerz, & Krüger, 2013; David & Cézilly, 2011; Martins, Roberts, Giblin, Huxham, & Evans, 2007; Schuett, Godin, & Dall, 2011), raising questions as to how this might directly or indirectly affect mate choice, fertilization

success, and/or parental care, and whether sexual selection contributes to maintaining inter-individual variation in personality traits (Schuett, Tregenza, & Dall, 2010).

In breeding zebra finches, personality may influence the speed and willingness with which an individual chooses a mate (David & Cézilly, 2011). Variation in female choosiness may be particularly relevant to variation in reproductive success when males and females are force paired in cages; very choosy females may simply abstain from copulating with the male she is provided. Over time, this could result in inadvertent selection for less choosy females in captive-bred populations (although the percentage of breeding failure in forced pairs in Table 1 suggests that females, despite being selected for generations for high breeding performance, are far from mating indiscriminately). There is as yet a paucity of data comparing mating behaviour of wild and domesticated females (Rutstein, Brazill-Boast, & Griffith, 2007). Future work comparing captive raised and cross-fostered individuals from several wild and domesticated populations should help to test whether variation in choosiness is more pronounced on the population or individual level and has changed in captivity, as has been demonstrated in the house mouse *Mus musculus* (Slade et al. 2014).

A more pressing question is whether non-random mate choice with respect to personality contributes to maintaining variation in these traits (Schuett et al., 2010). Both mate preference tests (Schuett, Godin, et al., 2011) and experimental pairing of in- and compatible personalities (see for improved reproductive performance e.g. Schuett et al. 2011b) should help answering these questions. In species such as the zebra finch with bi-parental care, mate choice based on assortative mating for personality could moderate sexual conflict in parental care leading to increased reproductive success (Royle, Schuett, & Dall, 2010). Therefore, pairs with similar

personalities may reproduce more successfully because that allows for greater coordination of reproductive and parental behaviours (Schuett et al. 2011b; Mariette & Griffith 2012b; but see Both et al. 2005; Schielzeth et al. 2010; McCowan et al. 2014). Housing practices that limit mate choice (e.g. forced pairing) could decrease overall reproductive success by preventing individuals from breeding with a complementary personality type.

Conditions experienced by individuals during development can have sustained effects on personality (reviewed in Stamps & Groothuis 2010). Therefore, it is possible that the variation described above in husbandry and housing conditions between laboratories generates personality variation that affects reproductive success. Unintentional selection for certain personality traits may result from biases in the individuals that cope better with captive conditions and breed successfully (McCowan et al., 2014), or those selected to breed or be part of an experiment. The extent to which these biases generally affect experimental outcomes remains to be determined, but could be an illuminating area of future research.

Developmental conditions can also directly affect an individual's mating behaviour and life-history more generally. Zebra finches imprint on visual and song phenotypes (Clayton, 1990b, 1990c; Immelmann, 1972) to an extent that subspecies specific preferences can be easily reversed (reviewed in Clayton, 1990a). Phenotypic quality also affects preferences: individual condition can influence female mate selectivity (Burley & Foster, 2006; Riebel et al., 2009) and also the specific choice of partner, with individuals pairing assortatively for quality (Holveck & Riebel, 2010). Recent work in the zebra finch has demonstrated striking relationships between the extent of loss of telomere length during early development and longevity (Heidinger

et al., 2012), and it is not hard to imagine that this will also affect an individual's reproductive investment strategy throughout life.

3. Population genetics and artificial selection

Zebra finches were first exported to Europe from Australia in the 1870's for the pet trade (Sossinka, 1970). Since that time, captive-bred zebra finches have been exported to North America and other parts of the world for breeding (Forstmeier, Segelbacher, Mueller, & Kempenaers, 2007; Zann, 1996) where they have subsequently been isolated to an unknown and varying degree at the local, national and continental levels. Domesticated zebra finches used in research in Europe and North America are mostly derived from populations maintained by amateur and professional finch breeders who have bred these populations for over a hundred years without an influx of wild-caught birds from Australia (Zann, 1996). Typically, captive zebra finches have not been bred with the intention of preserving genetic diversity and natural behaviour, because these are not priorities for the amateur and professional aviculturists who maintain most of the zebra finches in captivity (even though some laboratories may manage their stock to optimise these). Finch breeders are partly driven by the creation of new morphs that are selected by line breeding and back crossing, to the extent that there are now 30 recognized colour variants (Zann, 1996). Even 'wild type' birds are bred for competitive showing and judged against aesthetics and avicultural standards. As a result of this history, domestic populations may have diverged from their wild congeners, through artificial selection imposed by aviculture, natural selection to captive conditions (Gilligan & Frankham, 2003; Heath, Heath, Bryden, Johnson, & Fox, 2003), or through genetic drift (Woodworth, Montgomery, Briscoe, & Frankham, 2002). Two studies have found morphological differences

between wild and domesticated birds, and between different subsets of the domesticated population (Carr & Zann, 1986; Forstmeier et al., 2007). Reassuringly, despite this morphological divergence between populations, Tschirren et al. (2009) found that life-history trade-offs between traits were very similar between wild and domestic birds held in captivity. Even without intentional selection, the data we present (Table 1) illustrates substantial variation in reproductive success that could contribute to reduced genetic variation and population differentiation across and within laboratory populations.

To date, just a single study has addressed genetic divergence in the domesticated zebra finch. Forstmeier et al. (2007) used microsatellites to analyse 18 captive research populations and 2 wild populations. They found that all captive populations had lower allelic diversity than the two wild populations sampled and many populations showed strong differentiation from one another, particularly between the populations from different continents (Forstmeier et al., 2007). The limited neutral genetic divergence between populations observed by Forstmeier et al. (2007) does not exclude a higher degree of divergence in functional traits across these domestic populations that may determine some part of inter-population variation in reproductive performance. This is clearly an area that will benefit from the application of genomic tools that are becoming so well established in this species (Warren et al., 2010).

Although many studies work with ‘wild type’ birds, the presence of the colour variants in the background population, or directly in some studies, raises some issues. First, the degree of melanin pigmentation in animals (a likely target of much artificial selection) has been found to correlate with various life history traits (Meunier, Figueiredo Pinto, Burri, & Roulin, 2011), through trade-offs associated with the

melanocortonin system itself (Ducrest, Keller, & Roulin, 2008), and as a component of behavioural syndromes (Emaresi et al., 2014; McKinnon & Pierotti, 2010). In zebra finches, relatively few studies have specifically examined the effects of colour variants on behaviour or physiology, finding effects on sexual imprinting and song learning behaviour (Mann, Slater, Eales, & Richards, 1991; Vos, Prijs, & Tencate, 1993), and the visual system (Bredenkötter & Bischof, 2003; Eckmeier & Bischof, 2008).

Second, a recent molecular analysis found that white morphs represented a distinct genetic cluster, reflecting their history of selective breeding (Hoffman, Krause, Lehmann, & Krüger, 2014). In the process of selecting for these colour variants, there may have been unintentional side-effects on other traits, through genetic hitchhiking, selective sweeps, or epistasis. While there have been no investigations of this in the zebra finch, there are examples in other domesticated systems (e.g. rats: Will et al. 2003; Overstreet et al. 2005; dogs: Sutter et al. 2004). The effects of such genetic correlations in the zebra finch might be particularly likely, given that the genome of the domesticated zebra finch consists of few, relatively large linkage blocks compared to other vertebrate genomes (Backström et al., 2010).

Finally, the domesticated zebra finch represents a fragmented population with numerous barriers that reduce the free transfer of genes between different parts of the overall domesticated population across the world. As in small isolated populations in the wild, genetic inbreeding is a problem expected to cause a reduction in reproductive success (e.g. Billing et al., 2012; O'Grady et al., 2006a; Ralls, Ballou, Rideout, & Frankham, 2000). Although Forstmeier et al. (2007) found high heterozygosity within domesticated populations different levels of inbreeding may

still be responsible for variation in reproductive success between laboratories. Accurate genetic pedigrees are likely not available for all birds in most laboratories and for birds sourced from pet shops or finch breeders. As a result, it is difficult to completely evaluate the extent to which inbreeding effects might contribute to variation in reproductive success amongst different populations or laboratories. However, using the zebra finch as a model a recent study has demonstrated a new method for directly measuring the total amount of realised inbreeding (Knief et al. 2015), opening new opportunities for the study of inbreeding. Biologically, in domestic populations, inbreeding is a selective pressure (Ihle & Forstmeier 2013). Zebra finches actively avoid mating with familiar siblings (Ihle & Forstmeier, 2013), and full-sibling pairings suffer reduced reproductive success (Forstmeier et al 2012). Furthermore, the effects of inbreeding depression may emerge within a few generations in a small captive population of zebra finches, particularly on sexually selected and morphological traits, and in different populations, deleterious lethal alleles may have been purged out by breeding and previous population bottlenecks (Bolund et al., 2010). As stressful environments can exacerbate the effects of inbreeding (Armbruster & Reed, 2005), housing and other stressors that differ across laboratories might drive variation in the effect of inbreeding depression across different studies. The extent to which inbreeding may be having detrimental effects on reproduction across laboratories remains an open question.

The rapidly reducing costs of population-level genomic analyses will allow future studies to provide insight into the way in which genetic factors and the domestication process may contribute towards variation in reproductive success across laboratories. The assembled zebra finch genome (Warren et al., 2010) provides a scaffold against which we can examine selection and differentiation on functional

loci in the genome in comparison with neutral regions (Balakrishnan, Edwards, & Clayton, 2010; Larson & Burger, 2013). Availability of genomic resources will also facilitate the use of genome-wide association studies (GWAS) (e.g. Metzker 2010; Davey et al. 2011; Ekblom & Galindo 2011), and transcriptome sequencing (e.g. Mortazavi et al. 2008; Wang et al. 2009; Ekblom et al. 2014) which will help in the identification of genes responsible for trait differentiation within and between populations. The genetic history of the domesticated zebra finch may be a determining factor underlying some of the variation in reproductive success across different laboratories. However, studies of this highly amenable laboratory model promise to lead the next generation of work in our understanding of functional genomics in birds. In both of these areas there are many exciting opportunities ahead.

4. Conclusions

The ease with which domesticated zebra finches breed in captivity, relative to other birds, have made them a model system for research across a diversity of fields. However, despite the amenability of domesticated zebra finches to captive conditions, we present data here showing a large amount of variation in reproductive success across research laboratories. Although this variation is often noted anecdotally, it has not been the focus of any studies to date. Here, we have highlighted several potential factors that often vary between laboratories that could influence variation in reproductive success in domesticated zebra finches. We accept that there is always likely to be variation in the housing and husbandry practices of different laboratories. Research groups are often faced with constraints, and have to make strategic decisions on the basis of space or monetary considerations as well as following different opportunities to optimise local welfare considerations. Although more standardised

conditions across laboratories might be the most desired outcome, at the least we suggest that further consideration should be given to the way heterogeneity in conditions and protocols across different studies may affect outcomes and may provide insight into why laboratories can find conflicting results when approaching similar questions in the same species (Jennions, 1998; Seguin and Forstmeier, 2012).

Our review of the variation in reproductive success within and across laboratories highlights that studies of the captive zebra finch provide excellent opportunities to understand many aspects of reproductive biology, the sources of variation for fitness, and the mechanisms of the domestication process. We urge authors to bear these issues in mind when interpreting the findings of their studies on this important model species. We also believe that our findings, and future work on the questions we raise in this species, may provide broader insight into the issues that occur when animals are brought into captivity. This is relevant for fundamental animal-based research, but also for the breeding of animals in conservation programs that are increasingly called upon to establish source populations that provide organisms to re-establish or supplement wild populations.

Finally, we endorse the recommendation made by Kilkenny et al. (2010) in their paper outlining the ARRIVE guidelines for the reporting of information that will provide a greater degree of contextual information in a standardized way. Such information supporting future empirical zebra finch work will facilitate later attempts to review and analyse variation across studies.

Recommendation

We propose that all future work on captive zebra finches includes the information itemised in Table 4. We suggest that this data could be presented in a Table provided

either in the Methods section or as Supplementary material. The information requested in Table 4 is heavily informed by the items outlined in Kilkenny et al.'s (2010) ARRIVE Guidelines and their Table 2 with some additional information that is more relevant to the zebra finch (as discussed above). We advocate that the table be completed and used as is, rather than being modified with fields excluded or additional ones included. A standardised reporting form will facilitate future efforts to harvest and utilise the material presented.

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Figure Legends

Figure 1. In this illustrative example (not real data) the frequency distribution is illustrated showing the latency to lay after females are given the opportunity to breed. The population is divided into two categories (shaded black an grey). The categories might relate to a nominal trait such as breeding experience together (none or some); age (first year birds or older); or the categorical division of a continuous trait like bill colour. In this example we have illustrated an experimental cut-off at day 15, which if applied would bias the sample in favour of the category of dark-shaded individuals.

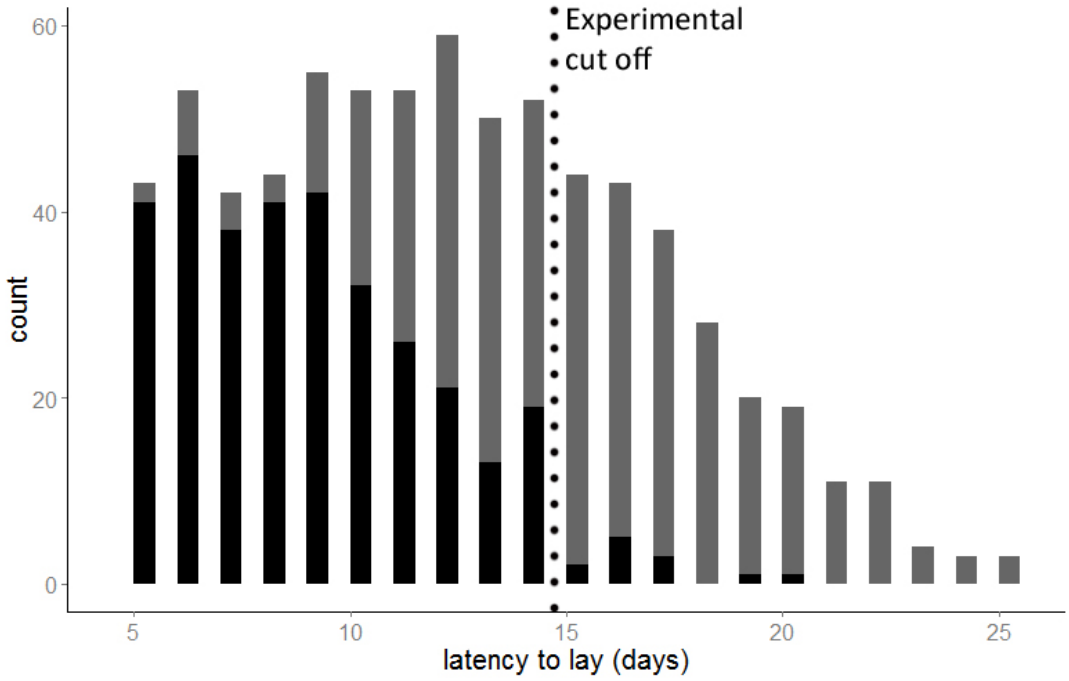
Figure 2. Mean number (± s.e.) of fledglings produced per successful brood across 29 females that were given the opportunity to breed repeatedly across a year, and that raised at least some fledglings successfully (7 females failed to fledge any offspring). All of these females were successful but there are significant differences in how many fledglings they produced when they fledged offspring (see results). All data were from the longitudinal study by Varian-Ramos et al (2014).

Figure 3. The proportion of females (± s.e.) that successfully fledge offspring when given the opportunity to breed, across different institutions.

Figure 4. The reproductive output of females when given the opportunity to breed measured through two metrics; producing a clutch (a & b), and producing fledglings (c & d). Females were examined across two categories: either force-paired or free-choice of partner (a & c); domestic or wild origin (b & d).

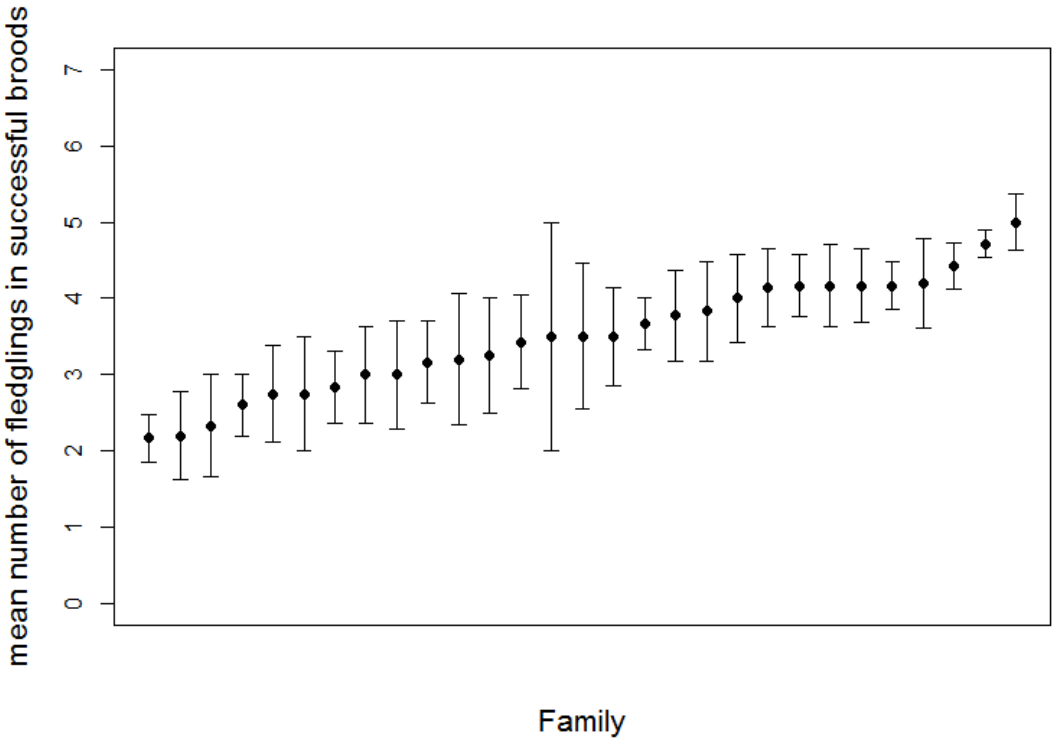
Figure 1

1535



1540

Figure 2.



1545

1550 Figure 3.

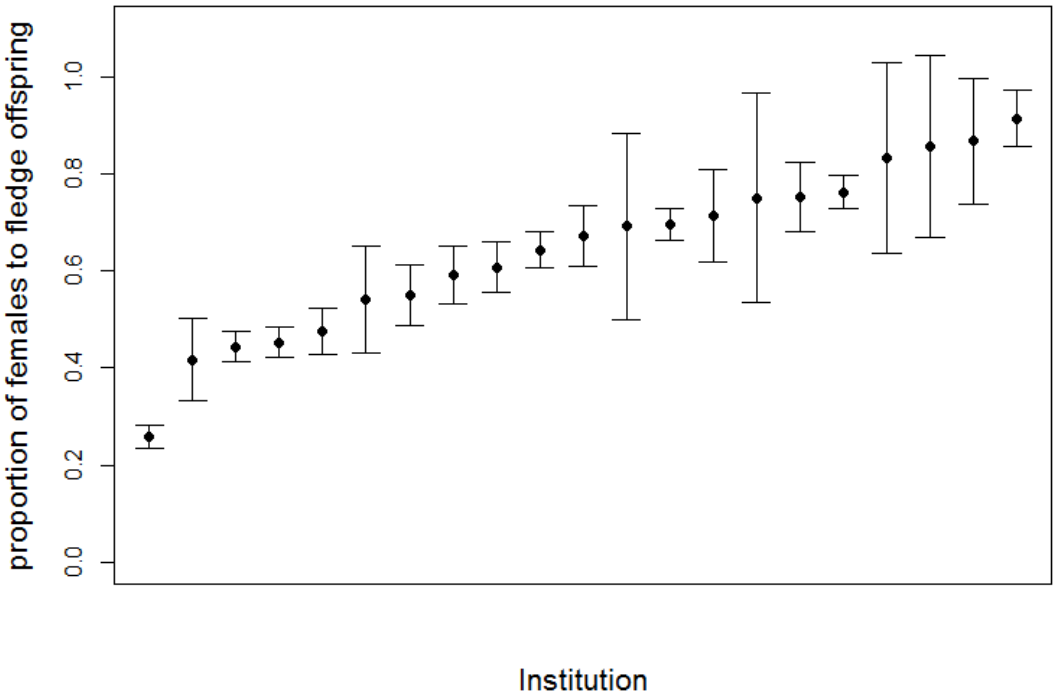
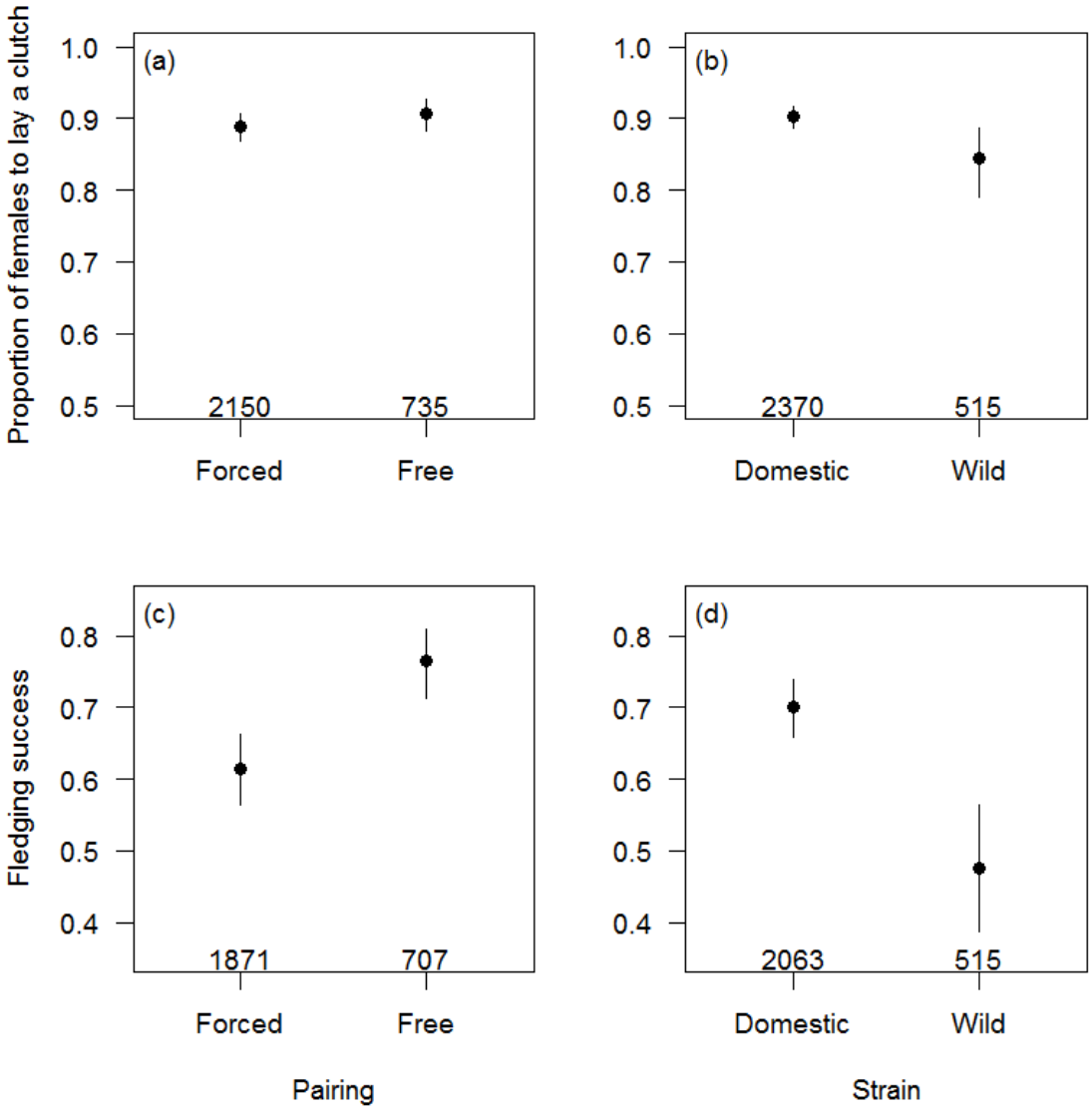


Figure 4.


Proportion of females to lay a clutch
(a)
1.0
0.9
0.8
0.7
0.6
0.5
2150
735
Forced
Free
(b)
2370
515
Domestic
Wild
Fledging success
(c)
0.8
0.7
0.6
0.5
0.4
1871
707
Forced
Free
Pairing
(d)
2063
515
Domestic
Wild
Strain